

**WEB CONSTRUCTION AND MODIFICATION
BY *ACHAEARANEA TESSELATA*
(ARANEAE, THERIDIIDAE)**

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ABSTRACT. The web construction behavior of *Achaeearanea tessellata* (Keyserling 1884) was observed in the field and in captivity using suspended wire frames that allowed detailed observations. Construction included three stages: preliminary exploration during which lines were broken, reeled up, and replaced; construction of anchor lines and the upper tangle; and construction and then filling in of the sheet below the tangle. Repeated visits to the mouth of the retreat during tangle construction resulted in the apparent reinforcement of the few lines radiating from this area, a possible adaptation to sense the location of prey in the web, and to facilitate orientation of the spider to prey in the web. Filling in the sheet, which alternated with additions to the tangle, included two previously undescribed behavioral patterns: irregular wandering on the sheet and apparent attachments of the dragline using only the two legs IV to hold previous lines against the spinnerets. The spider needed 1–2 nights, working several hours each night, to make a complete tangle and sheet and added lines and extended both the tangle and the sheet on subsequent nights. Spiders adapted the shapes of their webs to their surroundings.

Keywords: Web construction behavior, web design, aerial sheet web, cobweb spider

The spider family Theridiidae (cobweb or comb-footed spiders), which currently includes 2248 species in 87 genera, is one of the largest and most abundant groups of spiders (Forster et al. 1990; Agnarsson 2004; Platnick 2006). Theridiids construct a variety of webs (Wiehle 1931, 1937; Nielsen 1932; Benjamin & Zschokke 2002, 2003; Agnarsson 2004), most of which are three-dimensional and have often been described as irregular. Recent studies have shown, however, that the patterns of the construction behavior of some non orb-weavers are more regular than the apparent irregularity of their finished webs would suggest (Eberhard 1991; Benjamin & Zschokke 2002, 2003). The construction of non-orb webs is less well studied than orb web construction (Eberhard 1990b).

Species within the genus *Achaeearanea*, a relatively derived genus within the family Theridiidae (Agnarsson 2004; Arnedo et al. 2004), spin several types of webs. Apparently the most common are the gumfoot webs (Bristowe 1958; Agnarsson 2004), which are designed to trap walking prey. Gumfoot webs

are apparently ancestral in Theridiidae (Benjamin & Zschokke 2003; Agnarsson 2004). The sheet web of *Achaeearanea tessellata* (Keyserling 1884), in contrast, consists of a three-dimensional aerial tangle, containing a centrally located retreat for the spider and a tightly woven, more or less horizontal sheet near its lower edge (Eberhard 1972; see Benjamin & Zschokke 2003: fig. 6c). Flying prey that encounter the tangle fall to the sheet where the spider attacks them after having passed rapidly through the sheet itself (Eberhard 1972; Barrantes & Weng 2006). The related species *A. (= Theridion) japonica* (Bösenberg & Strand 1906) and *A. disparata* Denis 1965 build webs with apparently identical designs (Darchen & Ledoux 1978; Shinkai & Takano 1987). The report of a similar web in *Coleosoma blandum* O. Pickard-Cambridge 1882 by Benjamin & Zschokke (2003) was probably a mistake, due to a mix-up of specimens (Agnarsson pers. com.). The web of *A. tessellata* is mostly composed of non-sticky lines (Eberhard 1972), but there are also a few lines with small, scattered balls of apparently

viscous material (Barrantes pers. com.). There are descriptions of the construction behavior of several types of webs built by theridiids, synotaxids and the closely related linyphiids (Szlep 1965; Lamoral 1968; Eberhard 1976, 1995; Benjamin & Zschokke 2002, 2003, 2004). However, web construction behavior of theridiid aerial sheet webs has never been described. The present study provides a detailed description of the web building behavior of *A. tessellata* and reports modifications carried on the original web design to adapt it to the surroundings.

METHODS

Observations on the web building of *A. tessellata* were made between April and October 2004 in and near San José, Costa Rica. To observe construction behavior, 16 mature females were collected and transported (usually inside their retreats) to the laboratory. Some were kept in a 20 × 30 × 25 cm Perspex® box containing some pieces of wire to provide the spider with points to attach lines; some were placed on a *Yucca* sp. plant (Agavaceae), a species on which webs were commonly found in the field; and some were put on a three-dimensional construction of wire (diameter of wire strand approximately 1 mm) that hung on a nylon fishing line about 1.5 m above the floor. The spiders had difficulty climbing the nylon line and were thus (barring establishment of spanning lines using wind currents) relatively isolated from their surroundings but were nevertheless accessible for close observation. The spiders were fed one *Drosophila* every 1–2 days.

When mature female spiders were collected inside their retreats and the retreat with the spider was then placed on the substrate, the spider often began to suspend the retreat within one to two minutes independent of the time of day. All other behavioral observations were made between 19:00 and 24:00 h. Some night observations were made using a dim light that illuminated objects behind the web, thus making the silhouette of the spider visible. The spider was occasionally illuminated directly for a few seconds with a flashlight or a red laser pointer for more detailed observations. Other observations were made using the infrared “night shot” option of a SONY TRV 80 digital video camera. Both tangle and sheet construction behavior were taped (a total of

25 min). We observed at least parts of the construction of 20 webs in captivity and five webs in the field. Construction of webs in the field was induced by destroying part or most of the previous web. By turning on a light at night in the room with the spider, it was possible to inhibit web construction thus allowing us to lengthen or shorten the amount of time the spider had on a given night to work on its web. We did not attempt to measure durations of behaviors.

We measured 15 webs of mature females in the field, another 10 webs of mature females in captivity, and three webs of juveniles in captivity. We measured the “maximum length” of the sheet (not counting anchor lines extending beyond the sheet), and the “maximum width” perpendicular to this dimension. The height of the web was recorded from the sheet to the upper edge of the tangle. The variance of the ratio between maximum length and the maximum width in webs in the field and in captivity were compared with the Levene-Test (SPSS). Data were also checked for homogeneity of variances (t-Test, SPSS).

A voucher specimen of this study was deposited in the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica.

RESULTS

Web construction.—With the exception of lines laid to suspend the retreat, the entire web building process took place at night.

Preliminary suspension of the retreat: Mature female spiders collected inside their retreats usually started suspending the retreat shortly after being placed on the new substrate. After attaching the dragline to the retreat by touching her spinnerets against its surface and while holding the dragline with one outstretched leg IV, the spider climbed upward and attached the dragline to a strand of wire. She then walked back under the newly laid line and attached it again to the retreat, thus doubling the line. Then she returned to the wire strand and climbed a little higher and attached again, repeating this several times. By repeating this process and connecting the new lines with each other, the retreat was pulled into a hanging position a few cm above the substrate. Usually the spider stayed on one side of the cage, but in two cases she climbed up the opposite side and attached the dragline.

The spider then entered the retreat and did not resume construction until night.

Spiders with egg sacs or juveniles in their retreats ($n = 8$) did not abandon their retreats, and suspended them as just described. In contrast, each of the five adult females without egg sacs abandoned their retreats as soon as they were released ($P = 0.0008$, Fisher Exact Test). Three of them left the retreat and hid motionless under a piece of leaf or wire and waited there immobile until night. The other two climbed up a wire strand and constructed a few lines and hung immobile under these lines until night.

Preliminary exploration: Undisturbed spiders started web construction around 19:00 h, about 1 h after sunset. The adults without egg sacs explored the surroundings and those not in a cage moved up to 3 m before making a web. During the exploration stage, the spider sometimes broke the line on which she was walking, reeling it up and replacing it with her dragline as she moved. The spider also repeatedly attached her dragline to a plant leaf or wire strand and then dropped slowly 20–30 cm. If she reached an object below, she attached her dragline. Otherwise she climbed back up her dragline, packing it into a small white mass (Fig. 1), which she left attached to the line from which she had descended.

Construction of the anchor lines and the tangle: The first lines often extended up to 30 cm, and the web soon became three-dimensional. We could not discern a pattern in the lines laid at this stage. Both direct observations and video recordings showed that when attaching the dragline to another line, the spider held the dragline with one leg IV and grasped the other line with ipsilateral legs III and IV, bringing this line toward the spinnerets and at the same time moving her abdomen ventrally toward the line (Fig. 2). The spider walked underneath silk lines at all times, and held her dragline with the tarsus of one leg IV. Periodically she switched the leg IV that held the dragline.

Constructing an anchor line to the substrate or wire strand during tangle construction, the spider attached her dragline to the retreat or another web line and then moved to the end of a line attached to the substrate/wire strand, then moved further along the substrate/wire strand before attaching her dragline; she then returned along the newly laid line, doubling it

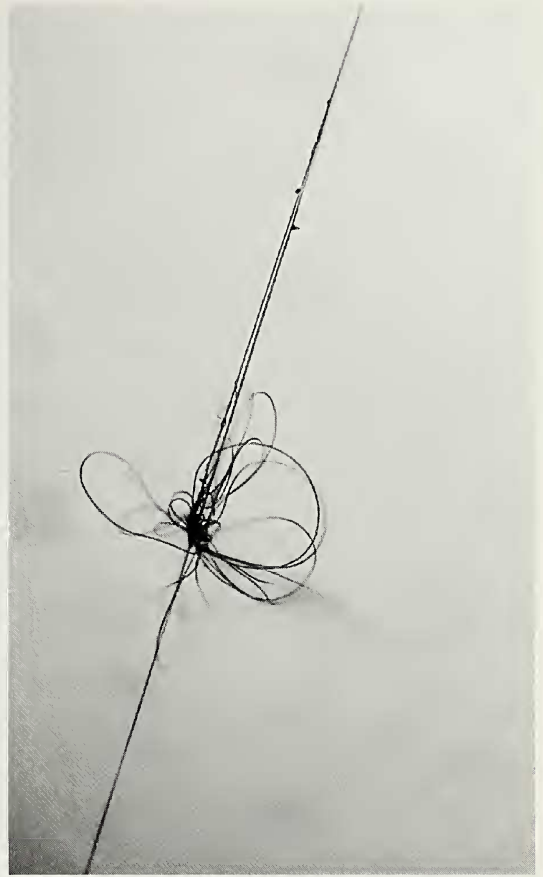


Figure 1.—Mass of loose silk seen under the compound microscope.

with her dragline. In attaching to a strand of wire, the spider often moved to the side of the wire away from the web before attaching; the new line was thus partially curled around the wire. Anchor lines and associated lines in a partially complete web included multiple lines that were more or less parallel and converged on the anchor (Fig. 7). The attachments of anchor lines in finished webs were heavily reinforced, consisting of multiple lines attached at slightly different points to the substrate/wire strand.

The spider repeatedly interrupted tangle construction to return to the mouth of her retreat, then left again to lay further lines. One spider returned to the mouth of her retreat an estimated 20–50 times during about 90 min of tangle construction. Despite these many trips to the mouth of the retreat, only a few lines connected the mouth with the tangle in a finished web (Figs. 11, 12). This probably re-

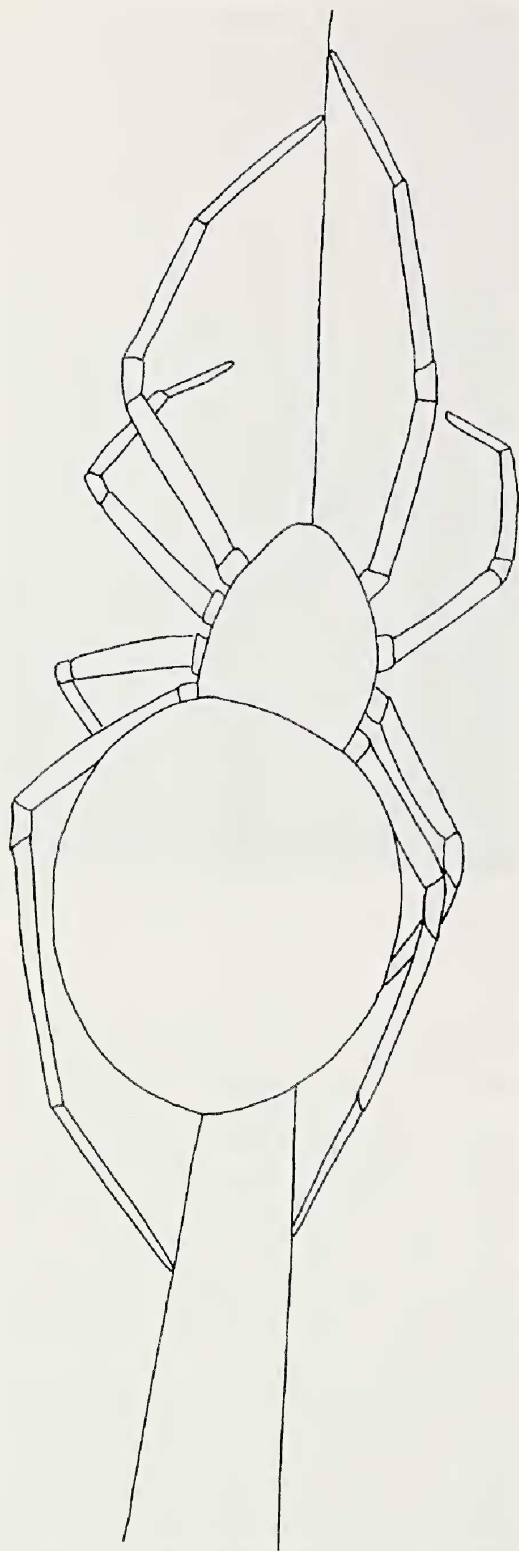
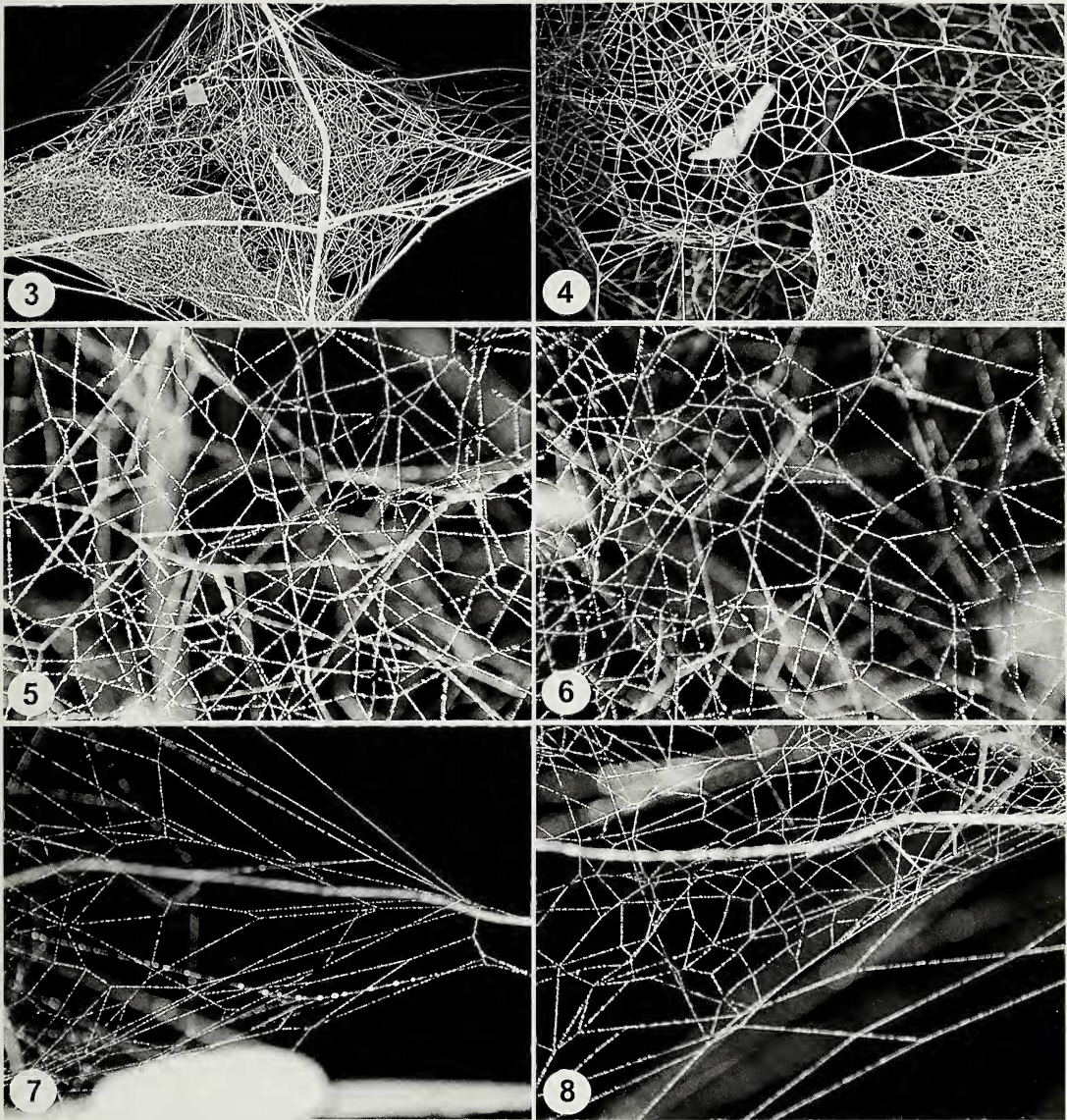


Figure 2.—Diagrammatic representation of the position of a spider attaching her dragline to another line.

sulted from the fact that the spider, when she returned to the retreat, consistently attached her dragline to the tangle 1–2 cm from the retreat, then moved directly to the retreat along a pre-existing line and attached her dragline again at the mouth of the retreat. When leaving to build more tangle, she reversed this process, attaching the dragline to the retreat mouth and then again only 1–2 cm from the retreat before moving away to resume tangle construction. Presumably these short lines laid near the retreat were generally laid along lines that were already in place; this would explain why there were few lines present in finished webs, despite the many visits to the retreat.

The spider made further descents during tangle construction. When she did not encounter substrate below, she climbed back up and moved on; leaving the white mass of packed up dragline silk attached to the tangle. The spider also sometimes broke lines in the tangle but simply released them and allowed them to sag loosely rather than reeling them up. One possible pattern in tangle construction was that more lines were laid above than below it during earlier stages, while more were laid below it later, but further observations will be needed to confirm this.

Construction of the sheet and filling in the sheet and tangle: The sheet was not built until an extensive tangle had been spun. When the spider was disturbed frequently during tangle construction by attempts to observe her with a light ($n = 7$ in captivity), no recognizable sheet was produced until the second night. Spiders allowed to build without serious disturbance produced both tangle and a sheet on the first night and then added more lines to both on the second night, so that they both became appreciably more dense ($n = 12$ in captivity, $n = 5$ in the field). Further construction was seen on the third night ($n = 8$ in captivity) and in two cases further extension and filling in also occurred on the fourth and fifth nights. During the later stages of filling in the sheet, the spider spent periods of up to 5 min walking under the sheet, apparently attaching her dragline to the sheet approximately 3–5 times each cm she moved (we could not see individual lines and presumed that attachments were made on the basis of the spider's behavior). Filling in the sheet and the tangle were not two discrete stages, but alter-

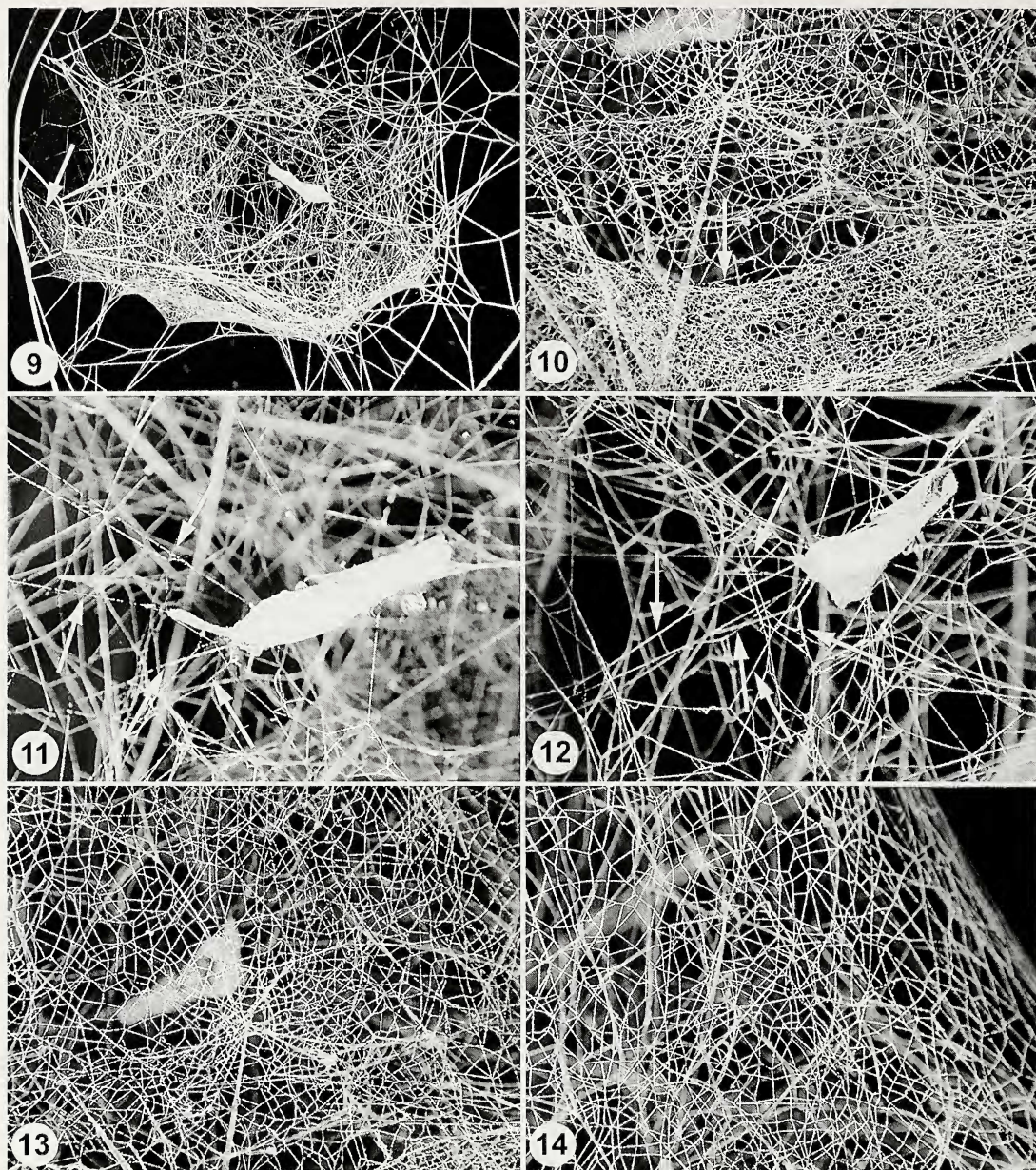


Figures 3–8.—Photographs of a partially complete repair of a web in which approximately half of the sheet was destroyed and the spider was allowed only about half the following night to repair it. 3. Ventral view of the sheet, showing a portion that was more than one week old (lower left) and the repaired portion built the preceding night (the thick lines are wire frame in which the spider built the web, and the object in the middle is the curled leaf retreat; the frame hung from a chain that is visible above the web); 4. Close-up of ventral view of the border between old and new sections of the sheet; 5, 6. Close-up views of the new area of the sheet, showing the substantial numbers of approximately parallel lines; 7. Close-up ventral view of an edge of the sheet where many more or less parallel lines converge on an anchor line; 8. Ventral view of an edge of the sheet where an apparent sharp turn-back by the spider is evident (arrow).

nated with one another. After a period of sheet construction, the spider usually climbed through the sheet and 1–2 cm up into the tangle, producing a line connecting the sheet to the tangle above, then either moved to a dif-

ferent region of the sheet or to the mouth of the retreat. In later stages of construction the spider appeared to dedicate longer periods of time to sheet construction ($n = 4$).

Apparently the general framework for the



Figures 9–14.—Photographs of a more completely repaired sheet, in which the spider was allowed the entire night to repair partial damage to a sheet older than a week. 9. Lateral view of web with sheet, and tangle and curled leaf retreat above the sheet. The arrow marks the upward lip at the edge of the sheet; 10. Ventral view of the border between previous sheet (below) and newly built repaired sector (above); 11–12. lines radiating from the mouth of the curled leaf retreat (arrows) in a tangle that was more than 1 wk old (sheet below the retreat was removed); 13–14. Ventral views of repaired sheet, showing diversity of tangle size and lack of consistently parallel lines in central portion of sheet (13) and near the edge where sheet turned upward (14).

sheet was laid out first, and then gradually filled in (Fig. 3). We were not able to distinguish, however, the first stages of sheet construction; it is possible that this was because

we did not observe spiders at the right stage of construction. We were not able to discern a pattern in the path the spider followed as she filled in the sheet, other than that she

sometimes seemed to spend time in only one part of the sheet, and then changed to work in another part of the sheet (Fig. 15). Photographs of one incomplete web suggested that the spider began to fill in the sheet in a more central area with a relatively sparse but evenly spaced array of lines (Figs. 3, 4) and then later included more peripheral areas and increased the density of lines (Figs. 13, 14). The sheet was not gradually extended in an orderly manner from a central point (as, for example, in the sheet-weaving theridiid, *Chrosiothes* sp. Eberhard, pers. obs.), nor did the spider move regularly from one edge of the sheet to another. Many of the relatively evenly dispersed lines in an early stage sheet were approximately parallel to each other (Figs. 5, 6), perhaps because of the pattern illustrated in Fig. 7. Further filling in of the sheet resulted in lines with a greater variety of orientations. Further observations are needed to check whether the patterns in Figs. 3–8 and 9–14 also occur in other webs.

Early in the construction of one sheet the spider made 180° turns repeatedly (Fig. 8), while later such turns were very rare as she wandered. At least in the later stages of filling in the sheet, this spider and others moved more rapidly in an irregular pattern, walking forward, sideways, and sometimes turning erratically in partial or complete circles (Fig. 15). While moving more or less laterally, the spider's lead leg I was often extended anteriorly and laterally and tapped actively. As she moved, the spider appeared to attach her dragline rapidly and repeatedly to the sheet (we could not see individual lines, however, and presumed that attachments were made because of the spider's behavior). Frame by frame analyses of video records revealed that as she appeared to attach her dragline, the spider sometimes held one leg IV behind her abdomen (presumably holding the dragline as during tangle construction), while the other leg IV and her ipsilateral leg III apparently held a line in the sheet; her spinnerets were pressed against the sheet between the tarsi III and IV when she tilted her abdomen laterally and ventrally (Fig. 16). In other presumed attachments made later during the construction of the same sheet, however, the spider's two legs IV apparently briefly grasped the sheet simultaneously on either side of her spinnerets and apparently pulled the sheet (or at least held it)

while her abdomen was flexed ventrally and the spinnerets apparently touched the sheet and attached her dragline (Fig. 17). The spider then moved onward with neither leg IV appearing to hold her dragline.

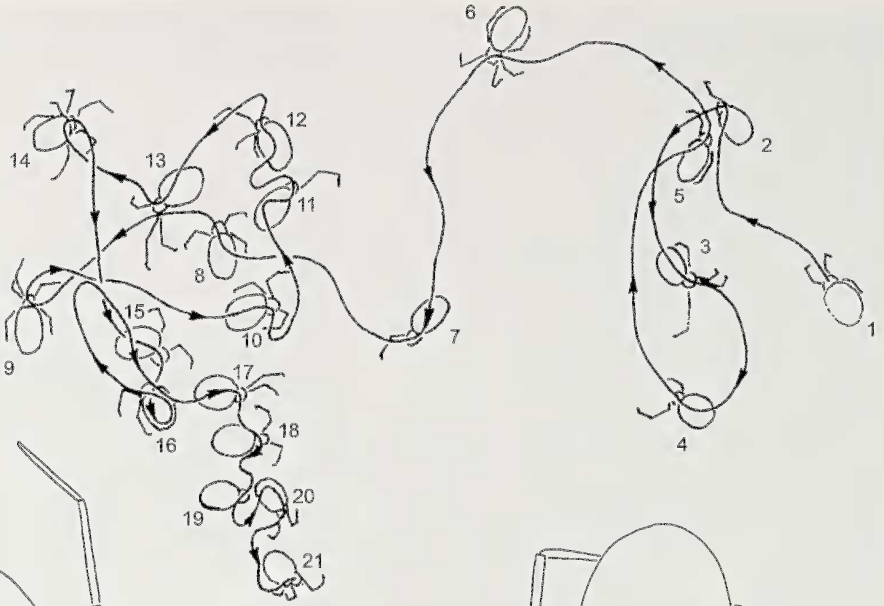
Although this second mechanism of bringing the spinnerets into contact with the sheet would seem imprecise in positioning the spider's spinnerets on a single line in the sheet, in a sample of 75 attachments on a finished sheet examined under a compound microscope, 66 were to a single line. Attachments were relatively dense. In one sheet that was more than a week old, there was an attachment disk in 77 of the 188 cases in which one line crossed another.

While filling in the sheet and the tangle during the first or subsequent nights, the spider also sometimes added new anchor lines from the tangle or from the sheet to the substrate/wire strands. Some additions resulted in extension of both the tangle and the sheet, including additions to the sheet with an upward tilt (arrow in Fig. 9). Web extensions were noted in seven cases. On one occasion the spider also adjusted the position of her retreat by pulling it a few mm higher and toward the middle of the web.

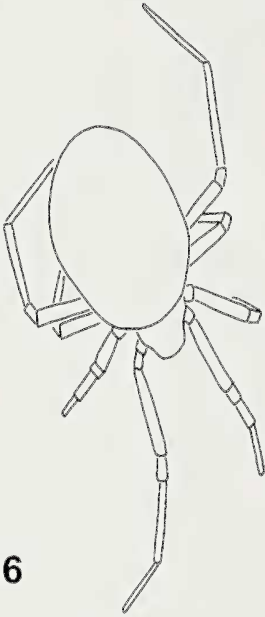
During all stages of construction the spider paused frequently to clean her legs. She stopped construction and passed the tips of her legs, one by one, through her mouth region. Legs IV were passed over the sides of her abdomen before being brought to her mouth.

General description of the web and variations.—The webs of adult females in the field were commonly attached to three to five relatively large, stiff leaves (e.g., *Agave* sp. plants) or to rigid branches. All webs in the field included a three-dimensional tangle with a dense horizontal sheet near its lower edge. The edges of the sheet often slanted upward approximately 1 cm (Fig. 9). The webs of the smallest juveniles with webs of their own (at least the first two instars are spent in the mother's retreat) had designs that were not distinguishable from those of adult females. Most webs (16 of 20) had a detritus retreat more or less in the center of the tangle, approximately five to ten cm above the sheet. Retreats were made of dry leaves (often curled) or other plant material. The spider rested upside down at the mouth of its retreat during the day. Spi-

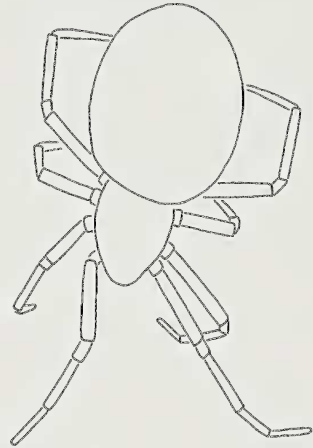
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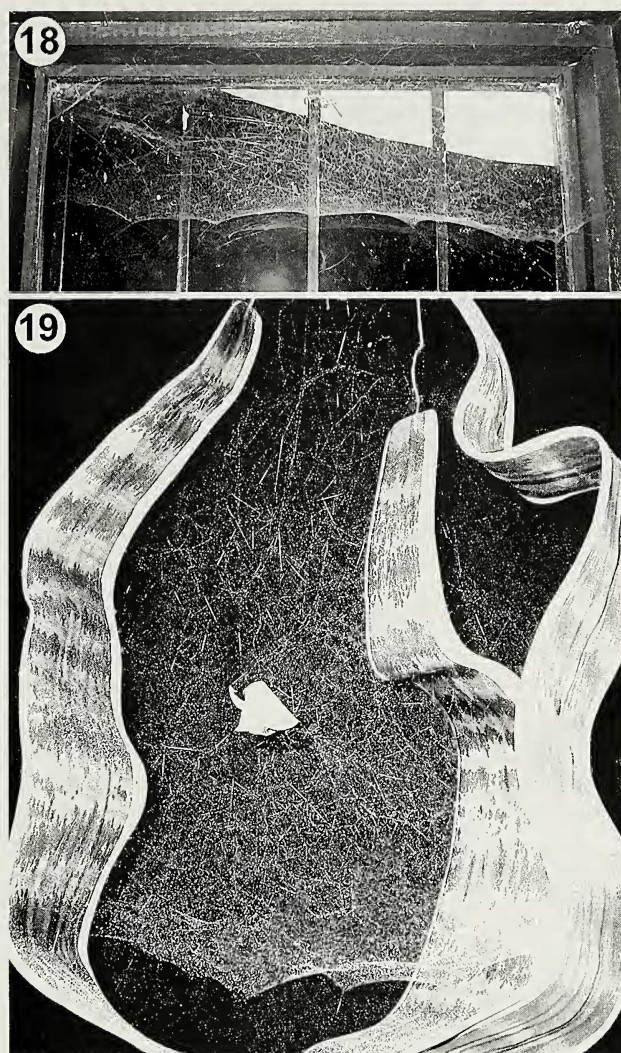


Figures 15–17.—Behavioral patterns during construction. 15. Path of a spider during 100 s of filling in the sheet as it wandered. The spider's position and orientation is shown every 5 s. When the direction of the path and the orientation of the spider's body are not the same, she was moving laterally rather than straight forward; 16, 17. Positions of spider during sheet filling-in behavior when she was apparently attaching her dragline to the sheet by holding a previous sheet line to her spinnerets with her ipsilateral legs III and IV (16) or with her two legs IV (17). (All traced from video images.)

ders without a detritus retreat rested at about the same position in the tangle.

The mean values (\pm SE) of web dimensions of adult females describe a more or less oval sheet, with a maximum length of 23.8 ± 8.9 cm and maximum width of 16.3 ± 4.5 cm; the mean height was 16.3 ± 3.5 cm. The height of the 15 webs in the field and the 10 in captivity ranged between 11.2–25.1 cm, while the maximum length and the maximum width measurements varied more (6.0–49.0

cm). The mean ratio of the two diameters did not differ significantly between field and captivity ($P > 0.05$, Levene-Test), but there was significantly greater variance in this ratio in webs built in captivity ($P < 0.05$). This was probably due to adjustment of web forms in captivity to unusual surroundings. The most striking examples of this were two webs with elongate and nearly rectangular sheets that were built in window frames. The most extreme web measured 49.0 cm in maximum



Figures 18, 19.—Web modification: 18. Elongated web built on a window frame; 19. More symmetrical web built subsequently by the same spider on a plant.

length and only 6.0 cm in the maximum width (Fig. 18). When this spider was then placed in a three-dimensional wire frame she built a much more typical web with a more or less oval 23.3×16.1 cm sheet (Fig. 19).

DISCUSSION

The absence of break and reel (or “cut and reel”) behavior during tangle and sheet construction in *A. tessellata* must be considered a design feature of their web construction behavior rather than an omission due to an inability to break and reel because *A. tessellata* broke and reeled lines with typical dexterity during exploration. Break and reel behavior occurs during

the construction of orb webs (Eberhard 1982, 1990a; Coddington 1986; Griswold et al. 1998), and is also performed by some other theridiids such as *Chrosiothes tonala* (Levi 1954) (see Eberhard 1991), *Phoroncidia studo* Levi 1964 (see Eberhard 1981), and *Argyrodes* sp. (Eberhard pers. obs.). Benjamin and Zschokke (2002, 2003) reported that they did not see break and reel behavior in *A. tepidarium* (C.L. Koch 1841) or *Steatoda triangulosa* (Walckenaer 1802). It is not clear if it also occurs in these species very early during web construction as in *A. tessellata* (only late in this study did we observe its occurrence). Breaking and reeling a line allows the spider to move points of attach-

ment and to adjust the tensions on newly laid lines; when a spider does not break and reel a line, in contrast, the line is reinforced. Perhaps web strength is more important than attachment or tension adjustments for *A. tessellata*.

Achaearanea tessellata also broke lines during tangle construction, but then released them to sag in the web, as also occurs in *S. triangulosa*, which cuts and bundles up old or loose lines (Benjamin & Zschokke 2002). These observations and observations of attack behavior (Barrantes & Weng 2006), also show that *A. tessellata* is able to cut lines rapidly and surely. The failure of *A. tessellata* to bundle up and remove these loose lines could be due to an inability to eat and recycle silk. Alternatively, perhaps the loose lines make the web a more effective trap, as with the "screw lines" of *Pholcus phalangioides* (Fuesslin 1775) (see Kirchner 1986).

Although *A. tessellata* was able to construct a functional finished web within 1–2 nights, webs in the field remained in place for up to several weeks during which time they were repaired and extended. Holes in the sheet resulting from prey capture were repaired the next night. Gradual accumulation of lines over periods of several days also occurs in several other theridiids (Szlep 1965; Lamoral 1968; Benjamin & Zschokke 2002, 2003; Barrantes pers. obs. on *Chrysso* sp.). In contrast, *Steatoda lepida* (O. Pickard-Cambridge 1879), *Latrodectus mactans* (Fabricius 1775) (Lamoral 1968; but see Szlep 1965 on *Latrodectus* spp.), and *Synotaxus* spp. (Eberhard 1976, 1995) in the related family Synotaxidae (Agnarsson 2003) are reported to build a new web each night starting at nightfall.

Web construction by *A. tessellata* can be roughly divided into three stages: exploration, construction of the anchor lines and the tangle, and construction of the sheet and then filling in both tangle and sheet. However, these stages were not easily distinguishable, especially early in construction and sheet filling was frequently interrupted by additions to the tangle. Photographs of partially completed webs suggested further possible divisions in sheet construction behavior, including a very early stage of filling in that was concentrated in the central portion and a later addition to the sheet of upward sloping outer margins (Fig. 10). These preliminary suggestions require further confirmation.

Several details of construction by *A. tessellata* resembled those in other species of theridiids, as in *S. triangulosa*, *A. tepidariorum*, and *Theridion* spp (Benjamin & Zschokke 2002, 2003). *Achaearanea tessellata* built only at night, held its dragline with one leg IV during tangle construction, doubled new lines it attached to the substrate, used existing thread lines as scaffolding to expand the web, and did not break and reel lines during tangle and sheet construction. In addition, females of *A. tessellata* with egg sacs or juveniles in their retreats began construction by making anchor lines that connected the retreat to the substrate, as in *S. lepida*, *S. triangulosa*, and *Latrodectus* (see Szlep 1965; Lamoral 1968; Benjamin & Zschokke 2002). A further resemblance to *L. tredecimguttatus* (Rossi 1790) (see Szlep 1965) was that the upper portion of its non-sticky web (the tangle) was built before the lower portion (the sheet).

Several more general patterns of *A. tessellata* behavior also resembled those of other theridiids. Construction of tangle lines prior to building the sheet, repeated returns to the retreat during tangle construction, alternation between sheet and tangle construction, and additions to both tangle and sheet on subsequent nights all resemble similar overall ordering, alternation of activities, and gradual extension of tangle and gumfoot lines in *Latrodectus* spp., *S. triangulosa*, and *A. tepidariorum* (Szlep 1965; Benjamin & Zschokke 2002, 2003). The general patterns of an approximate but not strict ordering of behavioral patterns, and of gradual extension and filling in of the web over several nights are probably very ancient, as they are present in such distant relatives as austrochilines (Lopardo et al. 2003). If theridiids are derived from orb weavers (Coddington 1986; Griswald et al. 1998), whose construction behavior is much more rigidly ordered and in which gradual web extension does not occur, then these less ordered aspects of construction must be convergently derived in theridiids.

The behavior of *A. tessellata* as the spider approached and left the mouth of the retreat (attach dragline 1–2 cm away, walk directly to retreat and attach, then attach again only 1–2 cm from the retreat while leaving) was presumably responsible for the low number of short lines radiating from the retreat mouth in finished webs (Figs. 11, 12). This design may

explain the surprising ability of *A. tessellata* in retreats to orient their attacks in the direction of prey trapped in the web even before leaving the retreat (Barrantes & Weng 2006).

The relatively short exploration stage we observed is similar to that of *Steatoda triangulosa* (see Benjamin & Zschokke 2002) and of several other theridiids (Szlep 1965; Lamoral 1968). Exploration by *A. tessellata* in the field is undoubtedly sometimes much longer, however, as spiders presumably must search for rigid objects that they use to support their webs. The descents during exploration and web construction, which also occur in *L. tredecimguttatus* (see Szlep 1965) and *S. triangulosa* (see Benjamin & Zschokke 2002), probably inform the spiders of the presence of objects below to which they can attach or that they need to avoid (Szlep 1965; Benjamin & Zschokke 2002). The relatively short duration of exploration in captivity may be an artifact of the structural simplicity of the observation area in captivity (Benjamin & Zschokke 2002). However, one of our observation settings, a plant in the family Agavaceae, offered a similar complexity to that of natural sites, and exploration was not noticeably longer.

The homology of the sheet in *A. tessellata* to structures in the webs of other theridiids is not clear. All current evidence shows that the ancestral web design for theridiids is the gum-foot web (Benjamin & Zschokke 2003; Agnarsson 2004). Other species of *Achaeearanea* make various types of webs, including gum-foot webs, and many have very sticky lines, not sheets (Benjamin & Zschokke 2003; Agnarsson 2004). The lower web layer of the gumfoot web of *L. tredecimguttata* (see Szlep 1965) is structurally somewhat similar to *A. tessellata* sheets. Construction behavior is somewhat different, however, in *L. tredecimguttata*: the spider fills in this layer in a regular back and forth pattern of movements from retreat to periphery, rather than by wandering. The erratic wandering and the attachment of the drag line to lines held by both legs IV during sheet construction by *A. tessellata* (Fig. 15) have not, to our knowledge, been reported for any other theridiid species or, for that matter, for any other spider. Their functional significance is not clear.

Attachment of anchor lines by *A. tessellata* to the far side of objects such as wires probably makes the attachments more secure. This can

be appreciated by comparing an attempt to free a piece of adhesive tape stuck to a surface by pulling on it parallel to the surface, as compared with pulling on it perpendicular to the surface. Such “around the corner” attachments have apparently not been reported in theridiids, but similar attachments are made by araneoid orb weavers such as *Nephila clavipes* (Linnaeus 1767), *Leucauge marinana* (Taczanowski 1881), and *Plesiometa argyra* FO. Pickard-Cambridge 1899, and also by the more distantly related *Philoponella vicina* (O. Pickard-Cambridge 1899) (Uloboridae) and *Diguetia albolineata* (O. Pickard-Cambridge 1895) (Diguetidae) (Eberhard 1990a, 2001, pers. obs.). Some previous studies of theridiid web construction behavior were made in smooth-walled containers where this kind of attachment is not feasible; this may account for this behavior not having been noted before.

Achaeearanea tessellata of all ages always made the same basic web design with an extensive tangle above a dense, horizontal sheet. Under normal conditions the sheet was relatively round, but spiders modified the form of the sheet radically to adapt it to unusual conditions. The greatest modification of the form (to an approximate rectangle of 49 × 6 cm) resulted when a spider deserted a less restrictive building site to choose this unusual site on its own. Flexibility in web shape may be common in theridiids. The general design of different webs of the theridiids *Steatoda* (= *Teutana*) *castanea* (Clerck 1757) and *Latrodectus* spp. remained the same, but the shapes of their webs were influenced by the spaces in which they are built (Wiehle 1931; Szlep 1965). Benjamin & Zschokke (2003) also mention “variable behaviors to build successive webs,” although they do not specify species or behaviors.

This study is preliminary in many respects. Further observations on the first stages of sheet construction, the site of the first filling in of the sheet, the apparent attaching movements during sheet construction, as well as the significance of the frequent returns to the retreat during tangle construction and the possibility that different lines are laid under systematically different tensions (Lamoral 1968) are all needed.

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LITERATURE CITED

- Agnarsson, I. 2003. The phylogenetic placement and circumscription of the genus *Synotaxus* (Araneae: Synotaxidae) with a description of a new species from Guyana, and notes on theridioid phylogeny. *Invertebrate Systematics* 17:719–734.
- Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zoological Journal of the Linnean Society* 141:447–626.
- Arnedo, M.A., J.A. Coddington, I. Agnarsson & R. Gillespie. 2004. From a comb to a tree: phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* 31:225–245.
- Barrantes, G. & J. Weng. 2006. The attack behavior of *Achaearanea tessellata* (Araneae, Theridiidae). *Journal of Arachnology* 34:456–466.
- Benjamin, S.P. & S. Zschokke. 2002. Untangling the tangle-web: web construction behavior of the comb-footed spider *Steatoda triangulosa* and comments on phylogenetic implications (Araneae: Theridiidae). *Journal of Insect Behavior* 15:791–809.
- Benjamin, S.P. & S. Zschokke. 2003. Webs of theridiid spiders: construction, structure and evolution. *Biological Journal of the Linnean Society* 78:293–305.
- Benjamin, S.P. & S. Zschokke. 2004. Homology, behaviour and spider webs: web construction behaviour of *Linyphia hortensis* and *L. triangularis* (Araneae Linyphiidae) and its evolutionary significance. *Journal of Evolutionary Biology* 17: 120–130.
- Bristowe, W.S. 1958. *The World of Spiders*. Collins, St. James Place, London. 304 pp.
- Coddington, J.A. 1986. The monophyletic origin of the orb web. Pp. 319–363. *In* *Spiders Webs, Behavior, and Evolution*. (W.A. Shear, ed.). Stanford University Press, Stanford, California.
- Darchen, R. & C. Ledoux. 1978. *Achaearanea disparata*, araignée sociale du Gabon, synonyme ou espèce jumelle de *Achaearanea tessellata*, solitaire. *Revue Arachnologique* 1:121–132.
- Eberhard, W.G. 1972. Observations on the biology of *Achaearanea tessellata* (Araneae: Theridiidae). *Psyche* 78:209–212.
- Eberhard, W.G. 1976. “Rectangular orb” webs of *Synotaxus* (Araneae: Theridiidae). *Journal of Natural History* 11:501–507.
- Eberhard, W.G. 1981. The single line web of *Phoroncidia studo* Levi (Araneae: Theridiidae): a prey attractant? *Journal of Arachnology* 9:229–232.
- Eberhard, W.G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* 36:1067–1095.
- Eberhard, W.G. 1990a. Function and phylogeny of spider webs. *Annual Review of Ecology and Systematics* 21:341–372.
- Eberhard, W.G. 1990b. Early stages of orb construction by *Philoponella*, *Leucauge*, and *Nephila* spiders (Araneae: Uloboridae and Araneidae). *Journal of Arachnology* 18:205–234.
- Eberhard, W.G. 1991. *Chrosiothes tonala* (Araneae, Theridiidae): a web-building spider specializing on termites. *Psyche* 98:7–19.
- Eberhard, W.G. 1995. The web and building behavior of *Synotaxus ecuadorensis* (Araneae, Synotaxidae). *Journal of Arachnology* 23:25–30.
- Eberhard, W.G. 2001. Under the influence: webs and building behavior of *Plesiometa argyra* (Araneae, Tetragnathidae) when parasitized by *Hymenopimecis argyraphaga* (Hymenoptera, Ichneumonidae). *Journal of Arachnology* 29:354–366.
- Forster, R.R., N.I. Platnick & J.A. Coddington. 1990. A proposal and review of the spider family Synotaxidae (Araneae, Araneoidea) with notes on theridiid interrelationships. *Bulletin of the American Museum of Natural History* 193:1–116.
- Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society* (London) 123:1–99.
- Kirchner, W. 1986. Das Netz der Zitterspinne (*Pholcus phalangioides* Fuesslin) (Araneae: Pholcidae). *Zoologischer Anzeiger* 216:151–169.
- Lamoral, B.H. 1968. On the nest and web structure of *Latrodectus* in South Africa, and some observations on body colouration of *L. geometricus* (Araneae, Theridiidae). *Annals of the Natal Museum* 20:1–14.
- Lopardo, L., M.J. Ramirez, C. Grismado & L.A. Compagnucci. 2003. Web building behavior and the phylogeny of austrochiline spiders. *Journal of Arachnology* 32:42–54.
- Nielsen, E. 1932. *The Biology of Spiders*, With Special Reference to the Danish Fauna. Levin and Munksgaard, Copenhagen, Denmark. 723 pp.
- Platnick, N.I. 2006. *The World Spider Catalog*, Version 7.0. American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/index.html>.

- Shinkai, E. & S. Takano. 1987. Spiders. Shinrin Shobo, Ltd., Tokyo (in Japanese). 128 pp.
- Szlep, R. 1965. The web-spinning process and web-structure of *Latrodectus tredecimguttatus*, *L. pallidus* and *L. revivensis*. Proceedings of the Zoological Society of London 145:75–89.
- Wiehle, H. 1931. Neue Beiträge zur Kenntnis des Fanggewebes der Spinnen aus den Familien Argiopidae, Uloboridae und Theridiidae. Zeitschrift für Morphologie und Ökologie der Tiere 13:349–400.
- Wiehle, H. 1937. Die Tierwelt Deutschlands. Spinnentiere oder Arachnoidea. 26. Theridiidae oder Haubennetzspinnen (Kugelspinnen). Fischer, Jena 33:119–222.

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